

The influence of air pollution on moss - dwelling animals: 1. Methodology and composition of flora and fauna

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The influence of air pollution on moss-dwelling animals: 1. Methodology and composition of flora and fauna. - This paper is part of a study investigating the suitability of the moss-dwelling fauna to act as a monitoring system for air pollution effects. The strategy developed to study the influence of air pollution on the fauna is introduced and ecological aspects of moss-invertebrate associations are presented. An attempt is made to characterise the flora and fauna as encountered in mosses from tiles and walls. Finally, the overall floristic and faunistic composition are given (including a complete list of species).

Key-words: Moss-dwelling animals - Air pollution - Moss species - Moss-invertebrate associations.

INTRODUCTION

The survey of pollution levels and of their effect on the biosphere is necessary to prevent injuries both to ecosystems and to human health. The physical and chemical monitoring of a few important pollutants is already well established in environmental surveys. Single species' tests are the major tools for estimating damage from environmental stress (CAIRNS 1983). However, the degree of reliability to predict response at the community level is relatively small (OKKERMAN *et al.* 1991). To allow accurate predictions, the study of ecosystem disturbances should be based on a multispecies approach (including bioindicators, *sensu* ARNDT *et al.* 1987) and on the lowest possible taxonomic level.

Ecological monitoring has been poorly developed, although it is successfully used to indicate water quality ("Saprobien-system" described by KOLKWITZ 1959) and specific air pollutants (MUKAMMAL 1976; ARNDT *et al.* 1987). Lichens and mosses, for example, are often used in regional surveys to indicate SO₂ pollution (e.g. LE BLANC & DE SLOOVER 1970; HECK & BRANDT 1977). No equivalent monitoring system exists

for soil ecosystems. Knowledge about terrestrial invertebrates as indices of environmental quality is alarmingly poor (SCHUBERT 1985; ARNDT *et al.* 1987). As the soil and its associated fauna are very complex, the use of simply structured, but similarly composed communities may provide an alternative for studying pollution effects on soil ecosystems.

Animal communities of moss cushions could be used for this purpose. The moss-dwelling fauna has a close similarity with the fauna of soils (NICHOLAS 1975). Epilithic (living on or among stone) moss cushions are abundant in urban as well as in rural environments (GILBERT 1968), thus allowing for comparative studies. An advantage of the moss-dwelling fauna is its availability for experimental purposes. Tegulous (living on tiles; from Latin: *tegula* = tile) moss cushions, for example, can easily be manipulated in the lab (e.g. fumigation with gaseous air pollutants) or transplanted to sites with different environmental characteristics.

The suitability of the moss-dwelling fauna to act as a monitoring system for air pollution effects was studied near Zürich from 1982 to 1989. The study involved three main approaches: 1) survey of natural communities in epilithic moss cushions, 2) fumigation (with SO₂) and 3) exposure of tegulous moss-invertebrate associations to different levels of air pollution in the field. The present paper introduces biological aspects of moss-invertebrate associations. It then describes the strategy developed to study effects of air pollution on the moss-dwelling fauna. Finally, the flora and fauna of both epilithic and tegulous moss cushions is characterised, and a list of species is presented.

MOSS-INVERTEBRATE ASSOCIATIONS

1. THE MOSSES AND THEIR ASSOCIATED FLORA

Mosses can be classified into three groups according to their moisture demands (RAMAZZOTTI 1972). In man-made environmental regimes, mosses of RAMAZZOTTI's groups "intermediate" and "dry" find a large variety of artificial substrata to colonise (SEAWARD 1979). Thus, only "intermediate" and "dry" mosses are considered in the present study, while the third group ("moist" mosses) is disregarded. The "moss cushion microcosm" comprises an autotrophic (i.e. algae, lichens and liverworts) and a heterotrophic microflora (i.e. bacteria, yeasts, and filamentous fungi). The latter is responsible for the primary decomposition of organic matter in analogy to decomposition in the soil ecosystem (DAVIS 1981). Thus, it is possible that both the moss and its associated microflora influence the moss-dwelling fauna.

2. THE MOSS-DWELLING FAUNA

Invertebrates associate with mosses wherever these grow (e.g. STAFANSKI 1923; TRAVÉ 1963; NIELSEN 1967; MCINNES 1991). According to GERSON (1982), the moss-invertebrate community includes the following taxa: Protozoans, rotifers, nematodes, tardigrades, and arthropods (especially mites and insects). TRAVÉ (1963)

pointed out that there are two more or less mutually exclusive faunas on mosses: Protozoans, rotifers, nematodes and tardigrades belong to the aquatic, arthropods to the terrestrial fauna.

The fauna of moss cushions is affected by a large number of interrelated abiotic and biotic factors. The moisture content of the microhabitat, probably along with the amount of insolation, seems to be the most important factor influencing the moss-dwelling fauna (TRAVÉ 1963; RAMAZZOTTI 1972). General aspects of the surroundings (open or covered areas), topographical location (height above ground, inclination), type of wall (sunken, freestanding or building), solar radiation and temperature are thus important as they regulate the water supply and/or evaporation (NIELSEN 1967; BERTRAND 1975). The moss-dwelling fauna does not appear to be specialised on any particular moss species (RAMAZZOTTI 1972; PÉREZ-IÑIGO 1975; GERSON 1982; KATHMAN & CROSS 1991). This may be partly understood by considering the moss cushion as a suitable microenvironment for the microflora and microfauna rather than as a main food source. Human activities may affect the bryofauna directly (e.g. release of animal toxic compounds) as well as indirectly (e.g. by releasing phytotoxic compounds, or by offering artificial substrata such as walls and roofs).

MATERIAL AND METHODS

1. GENERAL STRATEGY

In accordance with DIAMOND (1986), the present study included the following approaches: a) a survey of natural communities (faunistic survey), b) exposure experiments (field experiments), and c) fumigation experiments with SO₂ (laboratory experiments). The faunistic survey carried out simultaneously at all sites (main faunistic survey) allowed the comparison of natural moss-dwelling animal communities subjected to different air pollution levels (STEINER 1994, 1995a). The reliability of community analysis (terrestrial fauna) based on one single sampling was assessed by a second faunistic survey, carried out partly in the same locations (STEINER 1995a). The reliability of results on the aquatic fauna was estimated by investigating long-term dynamics (1984-1989) as well as annual fluctuation (1983-1985) of nematode and tardigrade populations (STEINER 1995b). In the exposure and fumigation experiments invertebrate communities of tegulous mosses were exposed to different levels of air pollution in the field (tab. 1, STEINER 1995c), and to different SO₂ levels in fumigation chambers, respectively (STEINER 1995c).

The following taxa were considered: Rotifers, nematodes and tardigrades as representatives of the aquatic fauna, mites (with emphasis on oribatid mites), insects (with emphasis on springtails) and other arthropods as representatives of the terrestrial fauna. Identification to species level was carried out for nematodes, tardigrades, oribatid mites and springtails. Rotifers were analysed as a group because their determination is difficult (J. Donner, pers. comm.). Moss species were partially identified by E. Urmi and collaborators (Institut für Systematische Botanik).

2. STUDY SITE DESCRIPTION

The study was conducted at urban sites in the city of Zürich and at rural sites in the canton of Zürich (tab. 1). "Study site" refers to an ancient or actual air pollution recording site, as well as to its direct surroundings, expected to have about the same pollution levels as the recording site itself. All study sites are situated at altitudes between 400 and 550 m above sea level, except site "A", which lies at an elevation of 800 m.

Tab. 1

Annual mean values of gaseous air pollutants at the study sites (SO₂, NO and NO₂ in µg/m³, CO in mg/m³; Abbr. = abbreviations for study sites, as used in text and figures; Year = period of air sampling; Type of study: fs = faunistic survey of October 1984, s = supplementary faunistic survey of June 1987, e = exposure experiments, dyn = study of seasonal and long-term population fluctuations, fum = fumigation experiments; urb. cat. = urbanisation categories: uht = urban high traffic, ult = urban low traffic, rlt = rural low traffic; - : not measured).

Study sites	Abbr.	Year	Type of study	SO ₂	CO	NO	NO ₂	urb. cat.**
Rosengartenstrasse	R	82/83	fs, s, e	47	4.4	357	87	uht
Weststrasse	W	82/83	fs, s	50	5.6	236	79	uht
Stampfenbachstrasse	T	82/83	fs, s, e	44	2.5*	157	54	uht
Überlandstrasse	U	82/83	fs, s	28	2.4	166	66	uht
Büchnerstrasse	B	82/83	fs, s	43	1.6	54	56	ult
Eglistrasse	E	82/83	fs, s	29	1.4	58	53	ult
Kaserne	K	82/83	fs, s, e	45	1.4	45	56	ult
Seefeldstrasse	S	82/83	fs, s	31	1.2	51	50	ult
Bachtel	A	84/86	fs	12	0.3	6	15	rlt
Höri Berg	H	84/86	fs	7	0.4	22	28	rlt
Männedorf	M	84/86	fs	15	0.4	16	30	rlt
Oberstammheim	O	84/86	fs	12	0.3	9	28	rlt
Rämistrasse	Rä	82/83	e	35	6.1	217	64	uht
Forchstrasse*	F	82/83	e	31	1.9	93	62	uht
Clausiusstrasse	C	84/85	e	43	1.9	44	61	ult
Mythenquai	Y	82/83	e	28	1.2	66	48	ult
Unterer Letten*	L	82/83	e	26	1.1	54	48	ult
Letzibad*	Z	82/83	e	27	1.2	50	50	ult
Karl Staufferstrasse*	KS	82/83	e	26	1.0	36	43	ult
Dübendorf	D	82/83	e	21	1.3	48	55	rlt
Tänikon	Tä	85	e	12	-	-	21	rlt
Hohenbühlstrasse*	Dyn	82/83	dyn	36	3.4	178	66	uht
Birmensdorf	Bi	84/85	fum	12	-	17	26	rlt

Levels of gaseous pollutants at the sites "D", "Tä" and "K" were continually monitored by the Swiss Federal Laboratory for Material Testing and Research (in Dübendorf), and at site "Bi" by BLEULER & BUCHER (1984). Mean values for the sites A, "H", "M", and "O" were determined by a commercial institute of applied ecology (Oekoscience, Zürich). Pollution values for site "C" were given by HUTER (1986) and for sites other than those mentioned above by the Air Pollution Control Agency of Zürich (BACHMANN-STEINER *et al.* 1983).

*Annual mean values are estimated based on measurements and guidelines given by the Air Pollution Control Agency of Zürich (BACHMANN-STEINER *et al.* 1983).

**Urbanisation categories are defined according to traffic volume (BACHMANN-STEINER *et al.* 1983) and distance from the center of the city.

3. SAMPLING AND SAMPLE PROCESSING

Sampling for the main faunistic survey was carried out in October 1984, for the second (supplementary) survey in June 1987, and for the study of population fluctuations between 1983 and 1989. Fumigation and exposure experiments were performed between 1982 and 1985.

The sampling unit size used for the analysis of the aquatic fauna was fixed empirically. As a general rule, a sampling unit should measure at least 20 times the length of the animals to be collected (COCHRAN 1963). A sampling unit with a diameter of 11 mm (cores of ca. one cm²) for the aquatic fauna, and 25 mm (cores of five cm²) for the terrestrial fauna was considered to satisfy this criterion and was used throughout the study.

The influence of moss cushion characteristics (e.g. size, thickness, orientation) and of the season on the aquatic fauna had been analysed in preliminary studies (STEINER 1990). In addition, the distribution of nematode and tardigrade species was investigated at different strata of the habitat (i.e. within moss cushions, within walls, and within sites). Sampling plans were then defined according to the aims of the different approaches (STEINER 1994, 1995a, b, c).

Samples for both the aquatic and the terrestrial fauna were taken from the same moss with cylindrical steel corers and passed immediately into glass vials for transport to the laboratory. The following sample sizes were used: 1) main and supplementary faunistic survey: four cm² for the aquatic fauna, ten cm² for the terrestrial fauna; 2) dynamics of the aquatic fauna: five cm²; 3) fumigation and exposure experiments: one cm².

Extraction of the fauna started generally one day after sampling. The aquatic fauna was extracted using a modified version of OOSTENBRINK's funnel-spray method (STEINER 1990). Moss cores were moistened prior to extraction and were then mechanically macerated. After an extraction time of three days, the moss samples were analysed under a dissection microscope for remaining organisms. The extracted animals were killed in hot water (60°C for two min). After a minimum preservation time of one week in TAF (i.e. 14 parts formol 38%, four parts triethanolamine; 82 parts *Aq. dest.*), the total number of extracted animals was determined under a dissection microscope (magnification 40 x). Nematodes and tardigrades were dehydrated using the rapid method of SEINHORST (1959). A maximum of 300 randomly selected individuals per sample was permanently mounted in glycerine. Unidentified individuals were proportionally distributed to the taxa found in that sample.

Arthropods were extracted in a modified MACFADYEN extractor (BIERI *et al.* 1978), gradually raising the temperature from 22 to 32°C during the extraction time of six days. Samples were moistened by spraying water every 12 hours. For the last four hours the temperature was increased to 50°C. The extracted arthropods were collected in isopropanol and counted under a dissecting microscope (magnification 40 x). Macroarthropods could be identified directly, whereas microarthropods had to be pre-treated either with lactic acid or KOH. For identification, mites were temporarily

mounted in cavity slides. The immature stages of the Oribatulidae (Oribatida) were processed separately (STEINER 1989). Springtails were either mounted permanently in Hoyer (Berlese) medium, or for quick observation simply placed in cavity slides.

4. DATA PROCESSING

Whenever possible, unidentified individuals (mainly preimaginal forms) in a sample were assigned to related single taxa (STEINER 1989) or were proportionally distributed on groups of closely related taxa occurring in the same sample. Species with uncertain taxonomic status were treated as follows: the nematodes *Plectus acuminatus* Bastian and *P. cirratus* Bastian as *P. acuminatus s.l.*; *Plectus parietinus* Bastian and *P. silvaticus* Andr ssy as *P. cf. parietinus*; juveniles of the closely related species of the genus *Plectus*, as well as first larval instars of *Chiloplectus cf. andrassyi* (Timm) as "*Plectus* (larvae; undetermined)"; the Neotylenchidae as different taxa, although the *Neotylenchidae sp. 1* and *Neotylenchidae sp. 2* consisted only of larvae, the remaining taxa of adults; the tardigrades *Hypsibius convergens* (Urbanowicz) and *H. dujardini* (Doy re) as *H. convergens s.l.*; the oribatid mites of the genus *Scutovertex* as *S. cf. sculptus* Micha l, a species typical of the habitat considered in this study (S. Woas, pers. comm.).

The sign test was applied to compare the ratio of higher taxonomic categories (main taxa) in epilithic and tegulous moss cushions.

FLORA

Species composition of the samples (epilithic mosses) taken in the main faunistic survey of 1984 is presented in tab. 2. More than 90% of the moss species belong to the Dicrananae, a superorder comprising mosses of acrocarpous growth form. *Bryum argenteum* Hedw. and *Tortula muralis* Hedw., are the most frequent species, accounting for 44% of the total number of samples. According to GILBERT (1971), the dominance of *B. argenteum* indicates both polluted conditions and a high nitrogen supply. Many of the species listed in tab. 2 seem to be typical of urban stonework, and are ubiquitous species (GILBERT 1971). The study of the fluctuations of the aquatic fauna (STEINER 1994) was confined to a large moss cushion of the species *Homalothecium cf. sericeum* (Hedw.).

Tegulous moss species sampled during fumigation and exposure experiments (STEINER 1995c) were dominated by the cosmopolitan species *Hypnum cupressiforme* Hedw. s.l., *Tortula ruralis* G rtn. Meyer & Scherb., *Bryum capillare* Hedw. s.l. and *Caratodon purpureus* (Hedw.). A very similar flora is found in roof habitats in England (GILBERT 1968) and Germany (VON DER DUNK 1988).

FAUNA

1. GENERAL ASPECTS

The present survey is the first comprehensive study of the fauna of epilithic mosses in Switzerland. In the past, surveys were either restricted to one or two main

Tab. 2

Overall species composition of moss samples taken from tiles during fumigation and exposure experiments (102 and 393 samples, respectively), and during the survey of natural communities carried out in October 1984 (216 samples; epilithic mosses). Systematic categories are according to FRAHM & FREY (1983).

Moss species	Relative abundance (%)	
	Tegulous mosses	Epilithic mosses
SUPERORDER		
<i>Ceratodon purpureus</i> (Hedw.)	16.4	6.5
<i>Encalypta streptocarpa</i> Hedw.		0.5
<i>Tortula intermedia</i> (Brid.)		0.9
<i>Tortula muralis</i> Hedw.		19.4
<i>Tortula ruralis</i> Gärt. Meyer & Scherb.	16.6	
<i>Barbula fallax</i> Hedw.		0.9
<i>Barbula hornschuchiana</i> Schultz		0.5
<i>Barbula rigidula</i> (Hedw.)		12.0
<i>Barbula</i> sp.		0.5
<i>Schistidium apocarpum</i> (Hedw.)	8.4	11.6
<i>Bryum argenteum</i> Hedw.		25.0
<i>Bryum capillare</i> Hedw. s.l.	16.4	6.9
<i>Bryum</i> sp.		2.3
<i>Orthotrichum anomalum</i> Hedw.		1.4
<i>Orthotrichum diaphanum</i> Brid.		2.8
DICRANANAE Σ acrocarpous mosses	57.4	91.2
<i>Pseudoleskeella catenulata</i> (Schrad.)		0.5
<i>Amblystegium serpens</i> (Hedw.)		6.5
<i>Homalothecium</i> sp.		0.5
<i>Brachythecium</i> sp.	14.1	
<i>Rhynchostegium</i> sp.		0.5
<i>Hypnum cupressiforme</i> Hedw. s.l.	28.5	0.5
<i>Pylasia polyantha</i> (Hedw.)		0.5
HYPNANAE Σ pleurocarpous mosses	42.6	8.8

taxa, and/or the epilithic habitat was sampled only casually (AMMANN 1908; HEINIS 1908, 1910; GISIN 1943; SCHWEIZER 1949, 1951, 1956; BARTOS 1950; ALTHERR 1952; PSCHORN-WALCHER & GUNHOLD 1957).

A total of more than 230 taxa and close to 240'000 individuals was recorded (appendix k). Nematodes and tardigrades accounted for 75% of the total number of individuals. Diversity was highest within nematodes (56 taxa), followed by mites (47; ticks included, oribatid mites excluded), springtails and oribatid mites (39 each), arthropods (37; previous taxa excluded) and tardigrades (16). As low density species were by far more numerous than high density species, additional sampling would certainly reveal other species. Significant differences exist between the faunal composition of mosses from tiles and from walls. Among the aquatic fauna, nematodes dominate in epilithic mosses (sign test, $n=13$, $P < 0.05$), whereas tardigrades prevail in tegulous mosses (sign test, $n=16$, $P < 0.01$). Among the arthropods, mites (oribatid mites included) dominate quantitatively in mosses from walls (sign test, $n=13$, $P < 0.01$), whereas there was no significant trend for the ratio mites/springtails in mosses from tiles.

MAXIMUM DENSITY OF HIGHER TAXONOMIC CATEGORIES

Tab. 3

Maximum density values (number of individuals/cm²) of higher taxonomic categories in tegulous and epilithic moss samples (Ori: oribatid mites).

Taxon	Tegulous mosses	Epilithic mosses
Rotifers	192	97
Nematodes	354	879
Tardigrades	927	227
Springtails	53	388
Oribatid mites	15	89
Mites (Ori excluded)	2	30
Arthropods*	8	3

* Taxa above excluded.

Tab. 3 shows the maximum density of main taxa for tegulous and epilithic moss cushions. Maximum densities of moss-dwelling rotifers (NIELSEN 1967; WRIGHT 1991), nematodes (NIELSEN 1967) and tardigrades (RAMAZZOTTI 1972; MORGAN 1977) approximate those recorded in the present study. The density of moss-dwelling springtails was several times higher in the present study than is reported in the literature (BENGTSON *et al.*, 1974, as cited by GERSON, 1982).

Comparison of the moss-dwelling fauna (tab. 3) with the fauna of soil (PETERSEN & LUXTON 1982) shows similar density values for rotifers and mites. Values reported by PETERSEN & LUXTON (1982) for tardigrades (10 individuals/cm²) and springtails (70 individuals/cm²) are smaller than corresponding values in tab. 3, whereas the density of soil-dwelling nematodes (3'000 individuals/cm²) is about three times larger. Taking into account that soil samples are usually thicker than the moss samples (e.g. 1 - 2 cm in the present study), moss-dwelling invertebrates occur at higher densities (at least temporally) than soil-dwelling animals.

2. SPECIES COMPOSITION OF THE AQUATIC FAUNA

Rotifers

Rotifers were recorded in all epilithic moss cushions, as well as in all moss cushions on tiles, before the fumigation and exposure of the tiles started. The rotifers found in the present study belong mainly to the Bdelloidea. This group is especially abundant in bryophytes of the Temperate Zone (J. Donner, pers. comm.), and many bdelloid species have a cosmopolitan distribution (HYMAN 1951; DONNER 1965).

Nematodes

In tegulous mosses, bacterial feeders (i.e. Monhysterida, Araeolaimida, Rhabditida) were more abundant than predators such as *Paratiripyla intermedia* (Bütschli) and *Prionchulus muscorum* (Dujardin), fungivorous (e.g. *Aphelenchoides*, Tylenchidae, and Neotylenchidae) and omnivorous nematodes (Dorylaimidae).

Chiloplectus cf. andrassyi was the most abundant species, followed by *P. intermedia*, other species of the family Plectidae (Araeolaimida), *Tylocephalus auriculatus* (Bütschli) and *P. muscorum* (appendix b). In epilithic mosses, fungivorous nematodes were predominant with *Aphelenchoides sp. 5* being the most abundant species, except at site "Dyn". The high number of bacterial feeders in tegulous mosses and of fungivorous nematodes in epilithic mosses indicates that the microflora of the two habitats differs substantially.

Many of the numerically dominant species were also characterised by high frequencies in tegulous and/or in epilithic moss cushions (tab. 4). *Plectus acuminatus s.l.*, *P. parietinus*, *P. parvus* Bastian, *P. intermedia*, and *P. muscorum* seem to be ubiquitous (STEINER 1990). For *C. cf. andrassyi*, *Aphelenchoides sp. 4*, and *Aphelenchoides sp. 5* the actual distribution is unknown.

Nematodes are amongst the most numerous animals feeding on primary decomposers. By grazing on the microflora, nematodes can have considerable impact on the distribution and activities of bacteria and fungi (SCHIEMER 1982; ANDERSON 1988) and participate thus indirectly in the decomposition of dead plant material in the moss cushions.

Tab. 4

Moss-dwelling taxa frequently encountered (rf > 20%) either in tegulous (first sampling; 74 samples) or epilithic moss cushions (survey of natural communities; Ne and Ta: 120 samples, Ar: 96). (rf: relative frequency; Ne, Ta, Ar: nematodes, tardigrades, arthropods; - : not present).

Taxon	Tegulous mosses rf (%)	Epilithic mosses rf (%)
Ne		
<i>Plectus acuminatus</i> Bastian s.l.	43	12
<i>Plectus cf. parietinus</i> Bastian	16	38
<i>Plectus parvus</i> Bastian	26	34
<i>Chiloplectus cf. andrassyi</i> (Timm)	74	22
<i>Aphelenchoides sp. 4</i>	3	32
<i>Aphelenchoides sp. 5</i>	1	46
<i>Paratripyla intermedia</i> (Bütschli)	58	18
<i>Prionchulus muscorum</i> (Dujardin)	32	26
Ta		
<i>Macrobotus areolatus</i> Murray	69	4
<i>Macrobotus cf. artipharyngis</i> Iharos	50	-
<i>Macrobotus hufelandi</i> Schultze	78	44
<i>Macrobotus persimilis</i> Binda & Pilato	1	39
<i>Hypsibius convergens</i> Urbanowicz s.l.	28	30
<i>Hypsibius oberhäuseri</i> (Doyère)	27	30
<i>Milnesium tardigradum</i> Doyère	3	36
<i>Echiniscus blumi</i> Richters	68	2
Ar		
<i>Camisia segnis</i> (Hermann)	1	34
<i>Tectocephus sarekensis</i> Trägårdh	19	81
<i>Scutovertex cf. sculptus</i> Michaël	24	8
<i>Zygoribatula exilis</i> (Nicolet)	-	39
<i>Trichoribates cf. trimaculatus</i> (Koch)	-	52
<i>Eupodes sp.</i>	-	62
<i>Tydeus sp.</i>	-	35
<i>Bdella longicornis</i> (L.)	-	23
<i>Polyxenus lagurus</i> L.	-	31
<i>Xenylla brevisimilis</i> Stach	31	9
<i>Chironomidae sp.</i>	-	27
<i>Psychodidae sp.</i>	-	27

Tardigrades

The Eutardigrada represented the major class of the phylum Tardigrada (appendix c). This is mainly due to the sampling plan having been restricted to northerly exposed habitats. Heterotardigrada occur preferentially in moss cushions exposed to direct solar radiation (RAMAZZOTTI 1972), which agrees with the high frequency of *Echiniscus blumi* Richters in tegulous moss cushions (tab. 4). *Macrobotus hufelandi* Schultze was the most common tardigrade found in the present study (tab. 4, appendix c).

Most tardigrades listed in tab. 4 are cosmopolitan species (MAUCCI 1986). *Milnesium tardigradum* Doyère and certain *Macrobotus* species found in this study (i.e. *M. areolatus* Murray, *M. hufelandi*, *M. persimilis* Binda & Pilato, and *M. richtersi* Murray) are predators of the aquatic fauna. It is believed, however, that some *Macrobotus* species are actually non specialised feeders. For instance, individuals of *M. hufelandi* were observed to ingest filamentous algae. *Macrobotus cf. arti-pharyngis* Iharos, as well as *Hypsibius* spp. probably ingest bacteria and/or cell contents of algae, fungi or moss leaves.

3. SPECIES COMPOSITION OF THE TERRESTRIAL FAUNA

Arthropods were the most diverse phylum of the terrestrial fauna, but poorer in numbers than representatives of the aquatic fauna (appendix k). Four classes of arthropods (i.e. arachnids, crustaceans, myriapods, and insects) were encountered (appendix d to i). Annelids and molluscs were extremely rare in the present study and are disregarded.

Arachnids

Araneae, Pseudoscorpiones, Opiliones and Acari are the four orders of the class Arachnida recorded in the present study (appendix d to g). The order Acari is the largest group represented by the suborders Gamasida, Ixodida, Actinedida, and Oribatida. While the presence of Ixodida in the moss habitat was unexpected, representatives of the other suborders are known to dwell in mosses (GERSON 1969, 1982; GERSON & SEAWARD 1977).

Oribatid mites reached the highest numbers of all arthropod taxa (appendix e). Most of the recorded oribatid species are microphytophages or non-specialised feeders with holarctic to world-wide distribution (WEIGMANN & KRATZ 1981). Oribatulidae (nine species) and Tectocephidae (one species) were the numerically dominant families, while representatives of primitive oribatid families (supercohort Macropylides) were rare. Within the oribatid mites, five species are typical dwellers of epilithic or tegulous moss cushions (tab. 4). The most frequent and numerically dominant species in epilithic mosses (main survey of 1984) was *Tectocephus sarekensis* Trägårdh (tab. 4, appendix e), closely related to *T. velatus* Michaël (KNÜLLE 1954). The latter species is one of the most common mite species occurring

in the soil, and is believed to reach greatest numbers in dry habitats (PSCHORN-WALCHER & GUNHOLD 1957; MURPHY & JALIL 1964). The exclusive occurrence and high frequency of *T. sarekensis* in mosses from tiles and walls (appendix e, tab. 4) can be explained by its higher resistance to desiccation as compared with *T. velatus* (JALIL 1972). Along with *T. sarekensis*, *Zygoribatula exilis* (Nicolet) was the most abundant mite species in epilithic moss cushions (appendix e). This agrees with the composition of epilithic and corticolous (i.e. living on bark) mosses in the region of Zürich (PSCHORN-WALCHER & GUNHOLD 1957) and in several European countries (STRENZKE 1952; PSCHORN-WALCHER & GUNOLD 1957; TRAVÉ 1963). The relative abundance of *Trichoribates cf. trimaculatus* (Koch) and *Camisia segnis* Hermann was low (appendix e). Nevertheless these species were frequently encountered in epilithic moss cushions (tab. 4). While *T. cf. trimaculatus* is known to dwell in this habitat (STRENZKE 1952; PSCHORN-WALCHER & GUNHOLD 1957), *C. segnis* is usually found in corticolous lichens (LEBRUN 1976; ANDRÉ *et al.* 1984). *Scutovertex cf. sculptus* was the only oribatid species in tegulous mosses with a relative frequency > 20% (tab. 4). Its related species *S. minutus* (Koch) seems to be typical of roof habitats (STRENZKE 1952; SMRZ 1992). According to S. Woas (pers. comm.), the two species are likely to be mixed up, and notes on their ecology are probably not very specific.

Gamasid mites (nine families) only occurred at low population densities (appendix f), with *Asca aphioides* (L.) the predominant species. Several of the recorded gamasid species prey upon diverse bryophagous taxa (WALLWORK 1967; GERSON 1972), including members of the aquatic fauna, enchytraeids, mites, as well as on eggs and larvae of higher insects.

Actinedid mites are usually represented in moss cushions by numerous species (SCHWEIZER & BADER 1963), however, their ecology is almost unknown (ANDRÉ 1986). In the present study, actinedid mite numbers (appendix g) were lower than those of oribatid mites (appendix e), but higher than those of gamasid mites (appendix f), complying with findings by ANDRÉ (1975) for the fauna of corticolous lichens. Among actinedid mites, three families (Eupodidae, Tydeidae, and Bdellidae) seem to be typical of epilithic moss cushions (tab. 4). Eupodid mites were the second most frequent arthropods in this habitat. They probably prey on other mites as indicated by KRANTZ (1978) for an eupodid species dwelling in mushroom beds. According to H. André (pers. comm.), at least two different *Eupodes sp.* were sampled in the present study. The Tydeidae were the most diverse actinedid family (appendix g). This agrees again with findings for the corticolous fauna (ANDRÉ 1986). Tydeid mites probably prey on nematodes (SANTOS *et al.* 1981), which were very abundant in epilithic moss cushions of the present study (appendix b). The Bdellidae were dominated by the species *Bdella longicornis* (L.). This predatory species was common in epilithic mosses (tab. 4, appendix g) and was also found in terrestrial moss cushions (SCHWEIZER 1951). Predators like Bdellidae and Rhagidiidae (appendix g) probably form an important link between soft bodied oribatid mites on which they feed, and the larger carnivorous arthropods (WALLWORK 1967). As the latter group was scarce in epilithic and tegulous mosses (appendix d), the importance of predatory actinedid mites increases in these habitats.

Crustaceans

Only two copepods were found in epilithic mosses taken for preliminary studies. Malacostracans (i.e. isopods) were more abundant (appendix d). They were usually found under the moss cushions, using the moss as a refuge. According to GERSON (1982), copepods and malacostracans usually associate with aquatic mosses.

Myriapods

Chilopods and diplopods were collected in epilithic (appendix d) as well as in corticolous mosses (PSCHORN-WALCHER & GUNHOLD 1957). Predatory chilopods (i.e. Lithobiidae) and diplopods (other than *Polyxenus lagurus* L.) are probably occasional guests, while *P. lagurus* reached a relatively high frequency (tab. 4). According to DUNGER (1983), the latter species is typical of the corticolous habitat.

Insects

The Apterygota are usually more numerous in bryophytes than the Pterygota, with springtails representing the dominant group (GERSON 1982). In the present study, a total of 36 collembolan species of the suborder Arthropleona and three species of the suborder Symphypleona were recorded, most of them in epilithic moss cushions (appendix h). A similar species composition was found by GISIN (1943) on bark. *Xenylla brevisimilis* Stach was along with *S. cf. sculptus* the only arthropod species typical of tegulous mosses (tab. 4). According to ANDRÉ (1983), *X. brevisimilis* is frequently encountered in foliose lichens on bark. The high abundance of *Schoettella ununguiculata* (Tullberg) in the faunistic survey of 1984 is based on a single sample with an exceedingly high density (388 individuals/cm²), but frequency of this species was low (8%). Many species of springtails are non-specific feeders (HALE 1967; VISSER 1985), ingesting dead plant matter, bacteria and fungi (PETERSEN & LUXTON 1983). Since enchytraeids, earthworms and large diplopods are usually absent from moss cushions, the contribution of springtails in particular and arthropods in general to the decomposition of organic material is far greater in mosses than in soil. By their high motility, springtails also play an important role in the dispersal of the microflora (CHRISTEN 1975; PETERSEN & LUXTON 1982).

The Pterygota were represented by ten insect orders (appendix i). Dipterans were the most conspicuous holometabolous insects in epilithic mosses (tab. 4, appendix i). They represent the insect order most intimately associated with bryophytes, though some taxa of springtails show a similar degree of association (GERSON 1982). Larvae of many dipteran families, including Chironomidae, Psychodidae and Cecidomyiidae, are known to dwell in bryophytes (BRAUNS 1976; GERSON 1982).

CONCLUDING REMARKS

Although epilithic and tegulous mosses are climatically extreme habitats (TRAVÉ 1963; RAMAZZOTTI 1972), the inhabiting fauna was surprisingly rich in taxa.

Based on the relationship between sample size and species number (the probability of a species' presence increases with sample size), and taking into account that several taxa were ignored in the present study, about 350 to 600 species can be expected to be found in dry mosses of central Europe (STEINER 1990). The high diversity (appendix a-i) as well as the high densities of moss-dwelling populations (tab. 3) indicate that mosses provide – at least temporally – favourable conditions for the associated fauna.

The wide ranging distribution of several taxa is probably a result of their mechanism of dissemination. Moss-dwelling animals evolved different adaptive life forms (eggs, cysts, tuns) to resist desiccation. These may be blown away by wind and can potentially reach any suitable habitat. Therefore, differences between mosses from roofs and walls (tabs. 3 and 4, appendix), or between study sites of a regional survey (STEINER 1994, 1995a) are unlikely to originate from limits to dispersal. The influence of air pollution, season and/or other environmental factors on moss-dwelling invertebrate communities is investigated by STEINER (1994, 1995a, b, c).

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APPENDIX: SPECIES LISTS

Total number of individuals: Rotatoria (a); Nematoda (b); Tardigrada (c); Arachnida (Acari excluded), Crustacea, and Myriapoda (d); Oribatida (e); Gamasida and Ixodida (f); Actinedida (g); Collembola (h), "other Insecta" (i) and "all taxa" (k) sampled in tegulous moss cushions of the fumigation and exposure experiments (STEINER 1995c), as well as in epilithic moss cushions of the survey of natural communities (STEINER 1994; STEINER, 1995a), and of the study of seasonal and long-term population dynamics (STEINER 1995b). Since identification to species level was not possible within each taxonomic group, indicated values for "Σ Taxa" are minimal values. (n = number of individuals; % = relative number of individuals; - = not analysed; + = less than 0.5%; ult = urban low traffic sites).

(a) Rotatoria		Tegulous moss cushions		Epilithic moss cushions					
		n	%	Survey 1984 n	Survey 1984 %	Survey 1987 n	Survey 1987 %	Dynamics n	Dynamics %
Σ Rotatoria	Σ Individuals	29796	100	6052	100	-	-	3140	100
(b) Nematoda									
Monhysterida									
Monhysteridae									
		53	+	15	+	-	-	7	+
	<i>Eumonhystera</i>	4	+	61	+	-	-		
	<i>Eumonhystera cf. vulgaris</i> (De Man)	1	+	6	+	-	-	113	1
	<i>Geomonhystera</i>			293	2	-	-		
	<i>Geomonhystera australis</i> (Cobb)	157	+	792	4	-	-		
	<i>Geomonhystera villosa</i> (Bütschli)	695	2	126	1	-	-	1748	16
	<i>Theristus</i>					-	-	1	+
	<i>Theristus cf. vesentinae</i> Andrassy			3	+	-	-		
Araeolaimida									
Plectidae									
	<i>Anaplectus granulatus</i> (Bastian)	3	+	5	+	-	-		
	<i>Ceratoplectus armatus</i> (Bütschli)			32	+	-	-	14	+
	<i>Ceratoplectus armatus</i> (Bütschli)			6	+	-	-	1	+
	<i>Plectus cf. acuminatus</i> Bastian s.l.	3174	8	82	+	-	-		
	<i>Plectus cf. parietinus</i> Bastian	569	1	384	2	-	-	1102	10
	<i>Plectus parvus</i> Bastian	663	2	315	2	-	-	203	2
	" <i>Plectus</i> (larvae; undetermined)"	9122	24	1994	10	-	-	2995	27
	<i>Chiloplectus cf. andrassyi</i> (Timm)	13276	34	590	3	-	-	2409	22
	<i>Tylocephalus auriculatus</i> (Bütschli)	1836	5	882	5	-	-	255	2
Chromadorida									
<i>Prodesmodora terricola</i> Altherr									
				4	+	-	-		
Rhabditida									
<i>Rhabditida sp. 1</i>									
	<i>Teratocephalus terrestris</i> (Bütschli)			1	+	-	-		
	<i>Teratocephalus terrestris</i> (Bütschli)			2	+	-	-	1	+
	<i>Eucephalobus</i>	1	+			-	-		
	<i>Eucephalobus striatus</i> (Bastian)	3	+			-	-		
	<i>Cephalobus</i>			8	+	-	-		
	<i>Acrobeloides</i>			2	+	-	-		
	<i>Ypsilonellus</i>					-	-	12	+
	<i>Ypsilonellus devimucronatus</i> (Sumenkova)	5	+	4	+	-	-		
	<i>Ypsilonellus vexilliger</i> (De Man)					-	-	1	+
	<i>Panagrolaimus</i>	18	+	291	2	-	-	115	1
	<i>Panagrolaimus cf. rigidus</i> (Schneider)	161	+	10	+	-	-	7	+
	<i>Panagrolaimus cf. rigidus</i> (Schneider)			107	1	-	-	19	+
	<i>Protorhabditinae sp. 1</i>			1	+	-	-		
	<i>Protorhabditis sp. 2</i>			27	+	-	-		
	<i>Mesorhabditinae sp. 1</i>			2	+	-	-		
	<i>Bursilla cf. monhystera</i> (Bütschli)			2	+	-	-		
Tylenchida									
	<i>Tylenchida sp. 1</i>	1	+	7	+	-	-	1	+
	<i>Tylenchida sp. 1</i>			1	+	-	-		

(b) Nematoda (continued)	Tegulous moss cushions		Epilithic moss cushions					
	n	%	Survey 1984		Survey 1987		Dynamics	
			n	%	n	%	n	%
Tylenchidae	7	+			-	-		
<i>Tylenchus arcuatus</i> Siddiqi			1	+	-	-		
<i>Tylenchus elegans</i> De Man			586	3	-	-		
<i>Filenchus</i>			5	+	-	-		
Haplolaimidae	2	+			-	-	10	+
Neotylenchidae			1	+	-	-		
<i>Neotylenchidae</i> sp. 1 larvae			209	1	-	-		
<i>Neotylenchidae</i> sp. 2 larvae			24	+	-	-		
<i>Neotylenchidae</i> sp. 3			16	+	-	-		
<i>Neotylenchidae</i> sp. 4			19	+	-	-		
Aphelenchoides	19	+	68	+	-	-	14	+
<i>Aphelenchoides</i> sp. 1	240	1	72	+	-	-	8	+
<i>Aphelenchoides</i> sp. 2			32	+	-	-		
<i>Aphelenchoides</i> sp. 3	17	+			-	-	3	+
<i>Aphelenchoides</i> sp. 4	31	+	2694	14	-	-	15	+
<i>Aphelenchoides</i> sp. 5	462	1	6736	35	-	-	633	6
<i>Aphelenchoides</i> sp. 6			507	3	-	-		
<i>Laimaphelenchus</i>	3	+	374	2	-	-	1	+
<i>Laimaphelenchus</i> sp. 1 (gr. pannocaudus Massey)			254	1	-	-		
<i>Laimaphelenchus deconincki</i> Elmiligy & Geraert			149	1	-	-	1	+
Enoplida								
<i>Paratripyla intermedia</i> (Bütschli)	6548	17	443	2	-	-	922	8
Dorylaimida								
Mononchidae	49	+	429	2	-	-		
<i>Prionchulus muscorum</i> (Dujardin)	956	2	144	1	-	-	63	1
<i>Nygolaimus</i> sp. 1			81	1	-	-		
Dorylaimidae	2	+	3	+	-	-	16	+
<i>Dorylaimidae</i> sp. 1			1	+	-	-		
<i>Dorylaimidae</i> sp. 2			45	+	-	-		
<i>Eudorylaimus</i> sp. 1			1	+	-	-		
<i>Eudorylaimus</i> sp. 2			53	+	-	-		
<i>Eudorylaimus</i> sp. 3			6	+	-	-		
<i>Eudorylaimus</i> sp. (gr. <i>carteri</i> [Bastian])					-	-	58	1
<i>Eudorylaimus</i> sp. (gr. <i>iners</i> [Bastian])					-	-	71	1
<i>Mesodorylaimus</i> sp. 1	19	+	1	+	-	-		
<i>Mesodorylaimus</i> sp. 2					-	-	6	+
<i>Mesodorylaimus</i> sp. 3					-	-	9	+
<i>Labronema</i> sp. 1					-	-	79	1
Nematoda (undetermined)	464	1	45	+	-	-	22	+
Σ Nematoda	Σ Individuals		38561	100	19054	100	10935	100
	Σ Taxa		21		47		26	
Nematoda treated as a group (ult)			12350					
(c) Tardigrada								
Heterotardigrada								
<i>Echiniscus blumi</i> Richters	6790	8	11	+	-	-		
<i>Echiniscus testudo</i> (Doyère)	146	+	887	10	-	-		

(c) Tardigrada (continued)	Tegulous moss cushions		Epilithic moss cushions					
	n	%	Survey 1984		Survey 1987		Dynamics	
			n	%	n	%	n	%
<i>Echiniscus trisetosus</i> Cuénot			42	+	-	-		
<i>Echiniscus</i>	16	+	1	+	-	-		
Eutardigrada								
<i>Macrobiotus areolatus</i> Murray	19829	24	192	2	-	-		
<i>Macrobiotus cf. artipharyngis</i> Iharos	16254	19			-	-		
<i>Macrobiotus hufelandi</i> Schultze	27535	33	2880	33	-	-	202	9
<i>Macrobiotus persimilis</i> Binda & Pilato	788	1	2177	25	-	-	722	33
<i>Macrobiotus richtersi</i> Murray			1	+	-	-	33	1
<i>Macrobiotus</i>	1972	2	533	6	-	-	16	1
<i>Hypsibius cf. bakonyiensis</i> (Iharos)								
<i>Hypsibius convergens</i> Urbanowicz s.l.	3191	4	132	2	-	-	291	13
<i>Hypsibius oberhäuseri</i> (Doyère)	6490	8	933	11	-	-	921	42
<i>Hypsibius cf. pallidus</i> Thulin	22	+	8	+	-	-	12	1
<i>Hypsibius</i>	139	+	16	+	-	-	8	+
<i>Diphyscon pingue</i> (Marcus)								
<i>Ishypsibius prosostomus</i> (Thulin)	30	+	279	3	-	-	10	+
<i>Milnesium tardigradum</i> Doyère	206	+	512	6	-	-		
Eutardigrada (undetermined)	9	+	3	+	-	-		
Σ Tardigrada	Σ Individuals		83612	100	8636	100	2215	100
	Σ Taxa		12		13		7	
Tardigrada treated as a group (ult)			2706					
(d) Arachnida (Acari excluded)								
Crustacea, and Myriapoda								
Pseudoscorpiones								
<i>Chthonius</i>			1	12				
Araneae								
Theridiidae			1	12				
Micryphantidae			2	25				
Linyphiidae			2	25				
Agelenidae			1	12				
Opiliones								
Phalangiidae			1	12				
Σ Arachnida	Σ Individuals		8	100				
	Σ Taxa		6					
Isopoda								
Oniscidae			24	100				
Σ Crustacea	Σ Individuals		24	100				
	Σ Taxa		1					
Chilopoda								
Lithobiidae			4	4			1	17
Geophilidae			7	7				
Diplopoda								
<i>Polyxenus lagurus</i> L.			1	93	88	29	100	8
Blaniulidae			1	1				

(d) Arachnida (continued)		Tegulous moss cushions		Epilithic moss cushions					
		n	%	Survey 1984 n	Survey 1984 %	Survey 1987 n	Survey 1987 %	Dynamics n %	
Pauropoda				1	1				
Σ Myriapoda	Σ Individuals	1	100	106	100	29	100	6	100
	Σ Taxa	1		5		1		2	
(e) Oribatida									
Brachychthoniidae						2	+		
<i>Liochthonius</i>				2	+				
<i>Verachthonius laticeps</i> (Strenzke)		2	+	10	+				
<i>Camisia segnis</i> (Hermann)				360	4	111	6	1	+
<i>Trhypochthonius tectorum</i> Berlese		283	30	221	2	3	+	16	5
<i>Damaeus</i>				3	+				
<i>Eremaeus oblongus</i> Koch				737	7	4	+		
<i>Tectocephus sarekensis</i> Trägårdh		197	21	5866	57	1126	60	112	37
Oppiidae				8	+				
<i>Oppia nitens</i> (Koch)						1	+		
<i>Opiella nova</i> (Oudemans)				3	+				
<i>Quadroppia quadricarinata</i> (Michaël)				8	+			114	38
<i>Oppia fasciata</i> (Paoli)				1	+				
<i>Suctobelba sarekensis</i> Forsslund				2	+				
<i>Cyberemaeus cymba</i> (Nicolet)		1	+	8	+	5	+		
<i>Micreremus brevipes</i> (Michaël)		1	+			1	+		
<i>Scutovertex cf. sculptus</i> Michaël		292	31	36	+	4	+		
<i>Dometorina plantivaga</i> (Berlese)				1	+				
<i>Oribatula tibialis</i> (Nicolet)				132	1	131	7		
<i>Phauloppia lucorum</i> (Koch)		18	2	57	1	170	9	2	1
<i>Phauloppia paspalevi</i> Csiszar				1	+				
<i>Scheloribates laevigatus</i> (Koch)				23	+				
<i>Scheloribates latipes</i> (Koch)		9	1	410	4	17	1		
<i>Zygoribatula exilis</i> (Nicolet)				1903	19	78	4	27	9
<i>Zygoribatula frisiae</i> (Oudemans)		6	1	15	+				
<i>Zygoribatula propinquus</i> (Oudemans)		5	1	58	1	20	1		
<i>Chamobates sp. 1</i>				3	+				
<i>Chamobates borealis</i> Trägårdh				36	+			10	3
<i>Ceratozetes cf. minutissimus</i> Willmann				1	+				
<i>Trichoribates cf. trimaculatus</i> (Koch)		92	10	213	2	193	10	10	3
<i>Mycobates parmeliae</i> (Michaël)		2	+						
<i>Minunthozetes pseudofusiger</i> Schweizer				136	1				
<i>Minunthozetes semirufus</i> (Koch)				5	+				
<i>Punctoribates punctum</i> (Koch)				6	+				
<i>Protoribates cf. capucinus</i> Berlese						1	+		
<i>Eupelops planicornis</i> (Koch)						1	+		
<i>Oribatella quadricornuta</i> (Michaël)				3	+				
<i>Galumna alatus</i> (Hermann)				8	+				
<i>Oribatida sp. 1</i>				1	+				
<i>Oribatida sp. 2</i>				1	+				
Oribatida (undetermined)		45	5					9	3
Σ Oribatica	Σ Individuals	953	100	10278	100	1868	100	301	100
	Σ Taxa	12		33		17		8	

(f) Gamasida and Ixodida

	Tegulous moss cushions		Epilithic moss cushions					
	n	%	Survey 1984		Survey 1987		Dynamics	
			n	%	n	%	n	%
G a m a s i d a								
Laelaptidae			5	5				
<i>Hypoaspis</i>	1	14						
<i>Hypoaspis claviger</i> Karg			3	3				
Phytoseiidae	2	29			1	11		
<i>Amblyseiulus</i>	1	14			1	11		
<i>Amblyseiulus murteri</i> (Schweizer)			5	5				
<i>Typhlodromus</i>	1	14						
<i>Typhlodromus andrei</i> Karg			9	8				
<i>Lasioseius fimetorum</i> Karg			3	3				
<i>Halolaelaps</i>			1	1				
<i>Asca aphioides</i> (L.)			33	30	4	44		
<i>Arctoseius cetratus</i> Sellnik			2	2				
Zerconidae			3	3				
<i>Zercon montanus</i> Willmann			3	3				
Rhodacaridae			2	2				
<i>Dendrolaelaps</i>			6	5	2	22		
<i>Gamasellus falciger</i> (Can.)	1	14						
Parasitidae			4	4				
<i>Pergamasus crassipes</i> (L.)			6	5				
Gamasina (undetermined)	1	14	12	11	1	11		
Uropodidae			6	5				
<i>Uroobovella notabilis</i> Berlese			4	4				
I x o d i d a								
Ixodidae			3	3				
Σ Gamasida + Ixodida	Σ Individuals							
	Σ Taxa	7	100	110	100	9	100	0
		4		12		3		0
(g) Actinedida								
Pachygnathidae			1	+				
Nanorchestidae	1	4	22	2	6	2		
Eupodes			454	36	71	27	4	8
Penthalodidae			1	+				
Penthaleidae			70	6				
Paratydaeolus			12	1				
Tydeidae	3	11	71	6	59	23	11	23
<i>Triophtydeus</i>			10	1				
<i>Microtydeus</i>			3	+				
<i>Tydeus bedfordiensis</i> Evans			14	1				
<i>Tydeus</i> (type <i>Lorryia</i> 2)			12	1				
<i>Tydeus</i> (Type <i>Paralorryia</i> 1)			9	1				
<i>Tydeus</i> (Type <i>Paralorryia</i> 2)			7	1				
<i>Tydeus</i> (Type <i>Tydeus</i> sp. V)			32	3				
<i>Tydeus</i> (Type <i>Tydeus</i> sp. A)			23	2				
Bdellidae	2	7	1	+			17	35
<i>Bdella longicornis</i> (L.)			103	8	17	7		
<i>Cyta</i>			65	5	2	1	1	2
<i>Spinibdellinae</i>	1	4	2	+				
<i>Cunaxidae</i>	4	15	13	1	26	10		
<i>Cunaxoides</i>			8	1				

(g) Actinedida	Tegulous moss cushions		Epilithic moss cushions					
	n	%	Survey 1984 n	Survey 1984 %	Survey 1987 n	Survey 1987 %	Dynamics n %	
Pygmephoridea			3	+				
Pygmephoridae			4	+				
Scutcaridae			1	+				
Tarsonemidae	1	4	289	23	1	+	1	2
Raphignathidae	1	4	2	+				
Cryptognathidae					2	1	4	8
Caligonellidae					2	1		
Stigmaeidae			5	+				
<i>Bryobia</i>			6	+	6	2		
Tenuipalpidae	1	4						
Eriophidae	1	4						
Erythraeidae	5	19			60	23		
Johnstonionidae					2	1		
Podotrombidiidae			1	+				
Trombidiidae	1	4	4	+	1	+		
Actinedida (undetermined)	6	22	8	1	4	2	10	21
Σ Actinedida								
Σ Individuals			1256	100	259	100	48	100
Σ Taxa	11		29		13		6	
(h) Collembola								
Arthropleona								
Hypogastrura			16	+				
<i>Hypogastrura</i> sp. 1					2	1		
<i>Hypogastrura assimilis</i> Krausbauer			5	+				
<i>Hypogastrura</i> cf. <i>elevata</i> Cassagnau			3	+				
<i>Hypogastrura engadinensis</i> Gisin			1	+				
<i>Hypogastrura tullbergi</i> Schäffer					25	12	47	73
<i>Hypogastrura vernalis</i> (Carl)			74	2	2	1		
<i>Schoettella ununguiculata</i> (Tullberg)			4047	88	52	25		
<i>Xenylla</i>			6	+				
<i>Xenylla boernerii</i> Axelson			1	+				
<i>Xenylla brevisimilis</i> Stach	1130	95	43	1	55	26	11	17
<i>Xenylla welchi</i> Folsom			11	+				
<i>Willemia anophthalma</i> Börner			1	+				
<i>Friesea claviseta</i> Axelson			31	1	1	+		
<i>Brachystomella parvula</i> (Schäffer)			4	+				
<i>Neanura muscorum</i> (Templ.)					1	+		
Onychiuridae			4	+	2	1		
<i>Mesaphorura</i>			6	+				
<i>Mesaphorura krausbaueri</i> Börner			20	+				
<i>Folsomides angularis</i> Axelson	18	2						
<i>Folsomia similis</i> Bagnall			3	+				
<i>Isotomiella paraminor</i> Gisin			2	+				
<i>Proisotoma hankoi</i> Stach					1	+		
<i>Isotoma arborea</i> (L.)			18	+				
<i>Isotoma viridis</i> Bourlet			1	+				
<i>Parisotoma notabilis</i> (Schäffer)			29	1	5	2		
<i>Isotomurus plumosus</i> Bagnall			1	+				
<i>Isotomurus palustris</i> (Müller)			6	+	1	+		
<i>Pseudisotoma sensibilis</i> (Tullberg)			2	+				

(h) Collembola (continued)

	Tegulous moss cushions		Epilithic moss cushions					
	n	%	Survey 1984		Survey 1987		Dynamics	
			n	%	n	%	n	%
<i>Entomobrya</i>			16	+	2	1		
<i>Entomobrya multifasciata</i> (Tullberg)			97	2	20	10		
<i>Entomobrya nivalis</i> (L.)			16	+	20	10		
<i>Entomobrya marginata</i> (Tullberg)			61	1	8	4		
<i>Orchesella</i>			1	+				
<i>Orchesella cincta</i> (L.)			25	1				
<i>Willowsia buski</i> (Lubbock)			35	1	4	2	3	5
<i>Willowsia nigromaculata</i> (Lubbock)			3	+				
<i>Lepidocyrtus</i>			2	+				
<i>Lepidocyrtus</i> gr. <i>servicus-pallidus</i>					1	+		
<i>Lepidocyrtus lignorum</i> (Fabricius)			1	+				
<i>Lepidocystus cyaneus</i> Tullberg			1	+				
<i>Pseudosinella</i>			12	+				
<i>Pseudosinella</i> sp. 1			4	+				
<i>Pseudosinella-Lepidocyrtus</i>			2	+				
Symphypleona								
<i>Sminthurinus</i>	10	1			1	+		
<i>Sminthurinus aureus</i> (Lubbock)			1	+				
<i>Sminthurinus bimaculatus</i> (Axelson)			3	+	4	2		
<i>Bourletiella</i>					1	+		
Collembola (undetermined)	36	3	2	+			3	5
Σ Collembola	Σ Individuals		4617	100	208	100	64	100
	Σ Taxa		32		18		3	
(i) Insecta (Collembola excluded)								
Diplura			2	1				
Psocoptera	4	10	7	4				
Thysanoptera			6	3				
Heteroptera			2	1	1	3		
Anthocoridae			1	1				
Homoptera								
Coccina			4	2				
Aleyrodina			5	3				
Aphidina			4	2				
Coleoptera								
Staphylinidae	1	3	4	2	2	5		
Curculionidae					1	3		
Ptiliidae					1	3		
Neuroptera								
<i>Chrysopa</i>					1	3		
Coniopterygidae			1	1				
Hymenoptera	3	8	1	1				
Mymaridae			8	4				
Braconidae			1	1				
Scelionidae			2	1				
Diptera	11	28	16	8	2	5	3	75
Chironomidae	19	49	41	21	20	50		

(i) **Insecta** (continued)

		Tegulous moss cushions		Epilithic moss cushions					
		n	%	Survey 1984 n	Survey 1984 %	Survey 1987 n	Survey 1987 %	Dynamics n	Dynamics %
Psychodidae				32	17	4	10		
Cedicomysiidae				17	9	3	8		
Sciaridae		1	3	20	10	1	3		
Scatopsidae				1	1				
Drosophilidae				1	1				
Trichoptera									
<i>Hydroptila sparsa</i> Curtis				2	1				
<i>Hydroptila pulchicornis</i> Pictet				1	1				
Lepidoptera									
Lepidoptera (larvae)				9	5	2	5	1	25
Insecta (undetermined)				1	1	2	5		
Σ Insecta	Σ Individuals	39	100	191	100	40	100	4	100
	Σ Taxa	5		21		10		2	

(k) **All taxa**

		Tegulous moss cushions	Epilithic moss cushions			Total
			Survey 1984	Survey 1987	Dynamics	
Σ Aquatic fauna	Σ Individuals	151'969	48'798	-	16'290	217'057
	Σ Taxa	34	61	-	34	72
Σ Terrestrial fauna	Σ Individuals	2'221	13'103	2'413	423	21'647
	Σ Taxa	36	133	62	21	162
Σ Aquatic + terrestrial fauna	Σ Individuals	154'190	6'421	2'413	16'713	238'704
	Σ Taxa	70	194	62	55	234